NEST TREES OF NORTHERN FLYING SQUIRRELS IN YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT—We examined nest tree preferences of northern flying squirrels (*Glaucomys sabrinus*) in an old-growth, mixed-conifer forest of Yosemite National Park, California. We tracked 8 individuals to 21 nest trees during July through September 2004. Flying squirrels selected nest trees that were larger in diameter and taller than either large nearest-neighbor or random trees. Flying squirrels showed no tree species preference, but used snags more often than live trees relative to their availability. Nest trees were not closer to perennial creeks than random trees. Results suggest that northern flying squirrels of Yosemite National Park might require large trees and snags, but unlike more xeric parts of the extreme southern Sierra Nevada, they might not be constrained by proximity to perennial streams.

RESUMEN—Examinamos las preferencias de árboles para nidos de las ardillas (*Glaucomys sabrinus*) en un bosque de árboles viejos de coníferas mixtas en el Parque Nacional Yosemite en California. Seguimos 8 ardillas a 21 árboles para nidos de julio a septiembre del 2004. Las ardillas escogieron árboles para nidos que fueron más grandes en diámetros y más altos que árboles grandes cercanos o árboles escogidos al azar. Las ardillas no mostraron preferencia para especies de árboles pero usaron árboles muertos más frecuentemente que árboles vivos en contraste a su disponibilidad. Los árboles para nidos no estuvieron más cerca de arroyos permanentes que árboles escogidos al azar. Estos resultados sugieren que las ardillas del Parque Nacional Yosemite requieren árboles vivos grandes y árboles muertos, pero diferente de que en áreas más secas del extremo sureste de la Sierra Nevada, podrían no estar restringidas por la proximidad a arroyos permanentes.

The northern flying squirrel is a forest-dwelling, arboreal mammal that reaches its southern distributional limit in the Sierra Nevada and Transverse Ranges of California (Wells-Gosling and Heaney, 1984). In the Sierra Nevada, the northern flying squirrel is a principal prey species of the California spotted owl (Strix occidentalis occidentalis; Williams et al., 1992) and an important prey to several forest carnivore species (Wells-Gosling and Heaney, 1984). The northern flying squirrel also is important as a dispersal agent of ectomycorrhizal fungi that

are critical for water and nutrient uptake in forest trees (Maser and Maser, 1988, Pyare and Longland, 2001). Because of their key role in forest food webs, flying squirrels are important for Sierra Nevada forest management (Williams et al., 1992), yet surprisingly little is known regarding the habitat and nest preferences of this species in California.

Most information on the nest tree preferences of the northern flying squirrels are based on studies in Pacific Northwest forests, where squirrels frequently use multiple nest trees each season and prefer to nest in tall and largediameter trees and snags (Carey et al., 1997; Cotton and Parker, 2000; Bakker and Hastings, 2002). In second-growth stands, flying squirrels can nest in smaller-diameter nest trees, but usually select the largest trees available (Mowrey and Zasada, 1984; Cotton and Parker, 2000). In the southern Sierra Nevada, flying squirrels frequently nest in both dead snags and live trees with cavities, but select snags over live trees when large-diameter snags are available (Meyer et al., 2005). Flying squirrels also select red fir (Abies magnifica) and prefer nest trees in close proximity to perennial creeks (Meyer et al., 2005), where food (i.e., truffles, canopy forage lichens) are in greater abundance than neighboring tree species or upland stands (North et al., 2002; Meyer and North, 2005).

The purpose of this study was to characterize nest-tree selection by northern flying squirrels in mesic old-growth mixed-conifer forest of the central Sierra Nevada and compare our findings to previous work on flying squirrels at more xeric sites in the extreme southern Sierra Nevada (i.e., Meyer et al., 2005). Our primary goal was to examine summer nest-tree use under more mesic forest conditions of the central Sierra Nevada, where average summer precipitation and canopy cover were 50% and 22% greater, respectively, than the xeric forest stands of the southern Sierra Nevada (Meyer et al., 2005). We predicted that flying squirrels would select 1) largerdiameter and taller trees, 2) snags over live trees, and 3) trees closer to perennial creeks, and 4) would have no preference for tree species in the absence of red fir.

We conducted this study at two 50-ha sites located 3 km apart along the west slope of Yosemite National Park. Elevation at each site ranged from 1,700 to 1,900 m. Yosemite has a Mediterranean-influenced montane climate, with hot, dry summers, and precipitation that falls almost exclusively as snow during winter (Major, 1990). Average summer (July-September) precipitation is 0.67 ± 0.15 SE cm at 1,600 m, and summer rainfall during this study was 0.32 cm. Both sites were dominated by largediameter (>100 cm) sugar pine (Pinus lambertiana; 48.5% of trees) and white fir (Abies concolor; 46% of trees), with a few large-diameter incense cedar (Calocedrus decurrens; 5% of trees) and ponderosa pine (P. ponderosa; 0.5% of trees). Both sites were old-growth forest containing

a multi-layered canopy and numerous large (>100 cm dbh) trees (many >200 years), snags, and decayed logs. Neither site had been burned for >70 years.

At each study site, we established a 7×15 grid (105 stations per site). Stations were 40 m apart and consisted of a single Tomahawk (Model 201) trap installed 1.5 m high on the trunk of a large (>70 cm dbh) tree (Meyer, 2003). From 7 June through 23 July 2004, we set traps in each plot for 5 consecutive nights for a total of 525 trapnights per site. We baited traps with a mixture of peanut butter and rolled oats. Traps were checked at dawn, closed during daytime, and reset at dusk. We marked captured animals with individually numbered, metal ear-tags, and body mass, sex, reproductive condition, and age class were recorded. We handled all captured animals in accordance with the American Society of Mammalogists Animal Care and Use Committee (1998), except that bedding material was not provided to reduce contact with rodent excreta as a safety precaution against hantavirus infection.

We fitted a subset of captured individuals (n =8) with a 3.5-g external radiotransmitter (<3% of body mass; model MD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) that was secured around the neck of each animal, and we tracked animals with hand-held receivers (Model TR-4; AVM Instrument Co. Ltd., Livermore, California). We tracked individuals to nest sites during the day, 1 to 3 times weekly from 25 July through 15 September 2004 (post-breeding period when young are weaned). We characterized nest trees by size (dbh), height, species, type (live tree or snag), and frequency of use. Additionally, we estimated canopy cover 1 m from the base of each nest tree (placed in a random cardinal direction) by using hemispherical photographs that were analyzed using Gap Light Analyzer 2.0 software (Simon Fraser University, Burnaby, British Columbia, Canada).

We recorded the geographic locations of all nest trees (±1 m accuracy) in UTM coordinates using a Trimble TDC-2 global positioning system (GPS) unit (Trimble Navigation, Sunnyvale, California). We used spatial UTM coordinate data to estimate the distance between nest trees and the nearest perennial creek using ArcView GIS 3.2a (Environmental Systems Research Institute Inc., Redlands, California). In those cases (12%) where the radio signal was equally strong between 2 trees, measurements were taken for

Table 1—Mean \pm SE of northern flying squirrel (Glaucomys sabrinus) nest tree and random tree (>50 cm dbh) variables in Yosemite National Park, California. P-values are based on independent t-test results (df = 40), with the exception of height, which is based on a dependent t-test (df = 20) between nest trees and large (>50 cm diameter) nearest neighbor trees.

Variable	Nest tree	Random tree	P-value
Diameter (cm) ^a	150.3 ± 9.8	91.5 ± 7.9	< 0.001
Height (m)b	51.0 ± 3.2	29.1 ± 2.5	< 0.001
Distance to creek (m)	323 ± 40	414 ± 48	0.161
Canopy cover (m)	73.3 ± 2.1	78.2 ± 1.4	0.133

 $^{^{\}rm a}$ 81% of nest trees were >120 cm dbh.

both trees and mean values were used for analysis. For distances <250 m between nest trees and a creek, we used a laser rangefinder (±1 m accuracy) to estimate distance.

To test if squirrels selected larger diameter and taller trees (relative to other trees in the immediate vicinity) for nest sites, we also recorded dbh, height, and canopy cover for the nearest 2 large (>50 cm dbh) trees or snags. To determine availability of live trees, snags, and different tree species, we measured vegetation at all flying squirrel capture locations (n = 13) and an equal number of random trap stations where no flying squirrels were captured (n = 26 total). At each of these locations, we recorded the total number of large (>50 cm dbh) trees of each species and the total number of large (>50 cm dbh) snags within a 12.6-m radius (0.05 ha) centered on the trap station. We compared the dbh and height measurements of nest trees and large nearestneighbor trees using a dependent t-test. We used an independent t-test to compare the dbh of nest trees and 21 large (>70 cm dbh) trees selected randomly from adjacent vegetation sample plots where flying squirrels were regularly captured (n= 26 plots).

We used Pearson's Chi-square (χ^2) to test the null hypotheses that flying squirrels showed no nest preference based on the type (snag versus live tree) or species of tree. We obtained tree availability data in these tests from the 26, 0.05-ha vegetation sample plots described above. To investigate and potentially minimize the effect of tree size, we conducted this analysis using trees >50 cm dbh. We used an independent *t*-test to determine whether nest trees were closer to creek areas than randomly selected trees. A total of 21 random trees was selected from a series of

random UTM-coordinates within our study site. We used an independent t-test to determine whether percent canopy cover of nest trees was different from the cover of randomly selected trees from nearby sample plots (all randomly selected trees were from independent plots). We tested all variables for normality with the Kolmogorov-Smirnov test and for homoscedasticity with Levene's test. We conducted all statistical tests with Statistica 6.1 (StatSoft Inc., Tulsa, Oklahoma), and differences were considered significant when P < 0.05.

We collared 8 flying squirrels (5 male, 3 female) and located them 107 times to 21 nest trees (all squirrels located >10 times, except one female located 8 times). Flying squirrels used 2.8 \pm 0.5 SE nests per month (males: 3.0 \pm 0.7; females: 2.3 ± 0.7). The diameter and height of nest trees were larger than random trees, although canopy cover and distance to creek were similar between nest and random trees (Table 1). The dbh of nest trees (150.3 \pm 9.8 SE cm) was larger than large nearest-neighbor trees $(82.6 \pm 6.4 \text{ cm}; t = 6.608, df = 20, P < 0.001) \text{ or}$ random trees (91.5 \pm 8.1 cm; t = 4.673, df = 40, P < 0.001). Relative to their availability (18.5%) snags and 81.5% live trees), snags (n = 12) were more commonly selected for nest trees than live trees $(n = 8; \chi^2 = 17.190, df = 1, P < 0.001).$ Species composition of nest trees was not different from larger (≥70 cm dbh), random trees ($\chi^2 = 4.411$, df = 2, P = 0.110).

Consistent with results from other studies, northern flying squirrels in old-growth mixed-conifer forests of Yosemite selected larger trees and snags for nesting. Northern flying squirrels also selected larger-diameter and taller trees in the southern Sierra Nevada (Meyer et al., 2005)

^b Mean \pm SE nest height was 31.5 \pm 1.9 m.

and northwestern British Colombia (Cotton and Parker, 2000), and larger-diameter residual snags or trees in western and central Oregon (Martin, 1994; Carey et al., 1997), southwestern Washington (Clark, 1995), and southeastern Alaska (Bakker and Hastings, 2002). Larger trees and snags can have more cavities for nesting (Carey et al., 1997), greater thermal insulation (Jeffrey, 2000), and reduced predation risk (Harestad, 1990; Carey et al., 1997).

Also supporting our predictions, flying squirrels in Yosemite preferred snags over live trees and showed no tree species preference in the absence of red fir. Sixty percent of nest trees used by flying squirrels were snags, although snags comprised only 20% of potential nesting structures at our sites. Flying squirrels likely selected snags because they offer more cavities for nesting than live trees (Meyer, 2003). Flying squirrels preferred to nest in large, residual snags over live trees in old-growth and secondgrowth forests of western Oregon (Carey et al., 1997), southwestern Washington (Clark, 1995), and the southern Sierra Nevada (Meyer et al., 2005). Flying squirrels also preferred snags and trees with dead tops and bole entries in southeastern Alaska (Bakker and Hastings, 2002).

In contrast to previous observations that flying squirrel nest trees are associated with perennial creeks in the southern Sierra Nevada (Meyer et al., 2005), flying squirrel nest trees in Yosemite were not associated with riparian habitat. Individuals near creeks can have greater access to drinking water and truffles than residents of neighboring upland areas (Meyer et al., 2005). Flying squirrels in the southern Sierra Nevada might have been more moisture-limited than populations farther north (i.e., Yosemite), where summer precipitation was 50% greater than in the Kings River watershed studied by Meyer et al. (2005). Alternatively, flying squirrels in the southern Sierra Nevada might not prefer nesting near riparian habitat per se, but could be attracted to red fir, a preferred tree species for nesting that is found predominantly in riparian drainages of mixed-conifer and red-fir forest (Meyer et al., 2005).

In agreement with Meyer et al. (2005), we recommend that forest managers consider retaining larger-diameter and taller trees and snags to provide suitable nest trees for flying squirrels in the Sierra Nevada. We also recommend that future studies of nest use by northern flying

squirrels in the Sierra Nevada examine nest use across 1) old-growth compared to managed (burned or mechanically thinned) forests, 2) multiple seasons, particularly in winter and spring when food availability (e.g., truffles) is low, and 3) other forest types, including ponderosa pine, red fir, and riparian forests.

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